J. HYM. RES.
Vol. 9(1), 2000, pp. 71–84

Afrotropical Ants (Hymenoptera: Formicidae): Taxonomic Progress and Estimation of Species Richness

Hamish G. Robertson

Life Sciences Division, South African Museum, P.O. Box 61, Cape Town 8000, South Africa; e-mail: hroberts@samuseum.ac.za

Abstract.—Forty-three of the 82 Afrotropical ant genera (52%) have been revised to modern standards resulting in a 50% increase in number of species. There are currently 1705 species of ants known from the Afrotropical region, a figure that could increase to over 2136 species if all ant genera receive a modern revision. To incorporate all undescribed species, total Afrotropical ant species richness was calculated by extrapolating from data on the proportion of undescribed species collected at Mkomazi Game Reserve in Tanzania and the Cape of Good Hope section of the Cape Peninsula National Park in South Africa. On this basis there are an estimated 3105 species of ants in the Afrotropical region, with 45% undescribed or currently occupying an infraspecific taxonomic rank. This extrapolation assumes that the average range sizes of described and undescribed species are similar, which in reality is unlikely because widely distributed species are more likely to have been collected and described. I present a method that distinguishes between widespread and localised species to correct for this problem, which extrapolates 4093 Afrotropical ants species, with 58% of species estimated to be undescribed or currently recognised only at infraspecific rank. It would take a highly productive systematist at least 21 years to complete revisions of the unrevised ant genera. A strategy is presented for improving specimen collection and taxonomy of Afrotropical ants.

Until recently, working on the taxonomy of ants and identifying them to genus was hindered by poor, out-dated catalogues and inadequate keys. Ant systematists, however, now have three books that provide a synthesis of our current knowledge: Bolton has produced keys to ant genera of the world (Bolton 1994) and a catalogue of world ants (Bolton 1995b) and Ward *et al.* (1996) have provided a thoroughly researched bibliography of ant taxonomic literature. In addition, the book by Shattuck (1999) makes identification of Australian ant genera much easier than before.

Despite the relative ease with which ants can now be identified to genus, species identification is much more difficult because many ant genera have not been recently revised. Species-level identifications in recently revised genera can also be problematic when such revisions are based on collections with limited geographic coverage that omit species and population variation. Older taxonomic works (mainly pre-1965) are difficult to use for identifying species because they are often burdened with poorly applied quadrinomials (genus, species, subspecies, variety) that do not correspond with evolutionary relationships. With the catalogue by Bolton (1995b), the bibliography by Ward *et al.* (1996), and a wealth of new material collected using modern survey methods, the tools are available to tackle the revision of neglected ant genera. However, at present there is no strategy in place for accomplishing this remaining work and basic information on approximately how much work remains is necessary for establishing goals and priorities. Although Bolton (1995a) has provided a taxonomic and zoogeographical census of documented ant diversity, he did not assess the current taxonomic health of all ants, nor does he address the issues of the proportion of ant genera that lack modern taxonomic treatment, and the effort that such treatment will require.

In addition to our inability to estimate the effort that will be required to revise all ant genera to modern taxonomic standards, we are also unable to reliably estimate how many ant species exist and how many are undescribed. On a world level, Gauld & Bolton (1988) estimated 15,000, and Hölldobler and Wilson (1990) estimated 20,000 species in total, these estimates being largely intuitive. By the end of 1993, 9538 described valid ant species in the world were recognised (Bolton 1995a), so according to the above two estimates, 36–52% of ant species either remain undescribed or currently occupy an infraspecific rank.

Estimates of total diversity are often made using data from particular localities where it has been possible to estimate the proportion of species that are undescribed, and to use this proportion to extrapolate to a wider level (e.g. Hodkinson and Casson 1991, Hodkinson 1992 for Hemiptera). This approach implies that the average range sizes of described and undescribed species are similar (Hodkinson and Hodkinson 1993; Hammond 1995). In practice, this is highly unlikely as widely distributed species are more likely to be captured and described than species with more localised distributions. Hodkinson and Hodkinson (1993) examined this problem by comparing data from two sites and providing a statistical test of whether the probability of capture of described species was different from the probability of capture of undescribed species and then using the ratio of these two probabilities to adjust the final estimate of species diversity. The outcome of such a comparison depends largely on the similarity and proximity of the two sites. An alternative approach, which involves distinguishing between widespread and localised species, is presented here to address the problem of range size differences between described and undescribed species.

The Afrotropical region is defined here according to Bolton (1994) as Africa south of the Sahara and the southern half of the Saudi Arabian Peninsula. Madagascar and its nearby islands are excluded. Our knowledge of the ant fauna of this region is the product mainly of the following taxonomists (see Ward *et al.* 1996 for publication details): F. Smith (1851–1879); Mayr (1853–1908); Forel (1869–1920's); Emery (1869–1926); Santschi (1906–1941); Arnold (1905–1962, including "A monograph of the Formicidae of South Africa", published 1915–1926); Brown (1943–1995); and Bolton (published 1969 to present).

The present paper is aimed at establishing the current level of taxonomic knowledge of Afrotropical ant species by assessing the proportion of ant genera that remain to be revised to modern taxonomic standards and the effort required to undertake these revisions. In addition, I estimate total ant species richness in the Afrotropical region using data on the proportion of undescribed species collected at two widely separated localities in Africa, namely Mkomazi Game Reserve in Tanzania and the Cape of Good Hope section of the Cape Peninsula National Park in South Africa. At both sites, ants have been intensively collected using a variety of methods, thereby increasing the probability that the observed ratio of undescribed to described species is a good estimate of the ratio for those species that have not been collected. I conclude by suggesting a strategy for improving both the collecting and the taxonomic treatment of Afrotropical ants.

METHODS

Estimation of species number increment from revision of genera.—I divided the Afrotropical ant genera between those that have received a modern revision (defined here as from 1965 onwards) and those that have not; revisions prior to 1965 are either incomplete or use the old quadrinomial system. Genera represented only by introduced species (*Linepithema humile* (Mayr), *Wasmannia auropunctata* (Roger)) have been excluded. Genera that have received a modern revision are henceforth referred to as 'revised genera' and the remaining genera as 'unrevised genera'. For each revised genus I calculated the species increment coefficient, i.e. the number of valid species divided by the number prior to revision. Descriptions of new species and the raising of subspecies to species increased the increment coefficient whereas synonymising of previously valid species decreased it. Lowering of rank from species to subspecies was not encountered in any of the revisions. In genera which have received more than one revision since 1970 (e.g. *Ocymyrmex*), I calculated the number of valid species before the first revision and the number by completion of the last revision. Subsequent papers describing additional new species in revised genera were also included in the analysis. An increment coefficient for all revised genera was calculated based on the total number of valid species before and after for all revisions and new descriptions.

For unrevised genera, I counted the number of valid species and multiplied this by the increment coefficient for revised genera to arrive at an estimate of the total number of species after revision. The total species for the revised genera plus this estimated value for the unrevised genera gives the 'Total estimated revised species'.

Estimation of total species richness.—An estimate of total ant species richness in the Afrotropical region was obtained by determination of the proportions of described and undescribed species in Mkomazi Game Reserve, Tanzania, and in the Cape of Good Hope section of the Cape Peninsula National Park, South Africa.

Ants were collected in Mkomazi Game Reserve using pitfall traps, malaise traps, Winkler bag leaf litter extractions, soil sieving, light traps, sweeping, and collecting by hand (Robertson 1999). Mkomazi Game Reserve has a wide range of vegetation types such as grassland, open and closed woodland, and hilltop forest. It lies in a region that does not have a long history of ant collecting although the vegetation types it contains have been sampled in other regions such as Kenya and Zimbabwe.

The Cape of Good Hope section of the Cape Peninsula National Park consists of mesic mountain fynbos, west coast strandveld and a few relict small patches of indigenous evergreen forest. Because of its position near the southern tip of Africa, many naturalists have collected in the Cape Peninsula and one might thus expect the ant fauna to be well known. However, many cryptic species went unnoticed until the recent systematic use of collecting methods such as pitfall trapping and Winkler bag leaf litter extraction.

For each of these two localities, I determined the ratio of undescribed species that belong to revised genera:

$$U/K = u/k$$

Therefore

$$U = u(K/k)$$

where U is the number of undescribed species in the Afrotropical region, u is the number of undescribed species at the locality, K is the number of known (i.e. valid) species in the Afrotropical region and k is the number of known species at the locality. As already discussed, this approach assumes that the average range size of known and undescribed species is similar (Hodkinson and Hodkinson 1993; Hammond 1995) which in reality is unlikely because widely distributed species would be more likely to have been collected and described. In order to reduce the bias, I arbitrarily categorised all known Afrotropical species in revised genera between 'widespread species' that have recorded distributions over three or more countries and 'localised species' that have been recorded from only one or two countries (based on information obtained from the revisions as well as from records in the South African Museum ant computer database). The average range size of the localised species is likely to be more similar to the average range size of the undescribed species than that of all known species together. By reducing the bias in this way, the ratio of undescribed to localised species at an Afrotropical level should therefore be similar to the ratio of undescribed to localised species at a local level and therefore

$$U = u(L/l)$$

where, for recently revised genera, L is the number of localised known species in the Afrotropical region and l is the number of localised known species at a particular locality.

Accumulation of described species as a function of collecting date.—As an alternative way of assessing the proportion of ant species that are still undescribed, for a sample of revised genera I recorded the year the type was collected for each valid species and plotted the accumulation of species as a function of collection date. The collection date was not recorded for many of the earlier types and for these I used the publication date instead. The early ant taxonomists such as Emery and Forel usually provided descriptions for new species within one or two years subsequent to their collection.

Time taken to revise genera.—In order to estimate the time that it would take to revise the unrevised ant genera, I analysed the productivity of the world's most productive ant systematist, Barry Bolton, who has also done most of the revisionary work on Afrotropical ants. During the 16 years from 1972 to 1987 he worked single-mindedly at revising various ant genera. For each of his taxonomic publications during this period, irrespective of whether they concerned Afrotropical ants, I recorded the number of valid species before the revision, the number of new species described and the number of valid species resulting from the revision. The number of valid species in an unrevised genus divided by the average number of initial valid species processed per year by Bolton, gives the number of years it would take to revise the genus (at maximum productivity).

RESULTS

Estimation of species number increment from revision of genera.—Modern revision of 43 (52%) of the Afrotropical ant genera has resulted in an overall 50% increase in number of species, so that the number of species at the completion of the revisions was 1.5 times greater than the initial number (Table 1). At the one extreme are genera such as *Anochetus*, *Psalidomyrmex*, *Pristomyrmex* and *Platythyrea* that decreased in number of species as a result of species being synonymised in the revision. At the other extreme are genera such as *Aximidris*, *Cyphoidris*, *Ocymyrmex*, *Paedalgus*, *Pyramica* and *Strumigenys* that more than doubled in size mainly as a result of the description of new species.

There are 862 valid species in the 39 (48%) unrevised Afrotropical genera (Table 2) and as the initial number of species in the revised genera amounted to 561 (Table 1), based on the relative number of species we are therefore about 39% of the way through revision of the genera to modern standards. Revision of the unrevised genera over a similar time period as the revised genera would have swelled the number of species from 862 species to about 1293 (Table 2). Together with the 843 species in the revised genera (Table 1) there is a total of 2136 estimated revised species, an increase of 20% over the 1705

Table 1. List of the Afrotropical ant genera that have received one or more modern taxonomic revisions (1965 onwards). The initial number of valid species before the first modern revision, the final number of valid species known at present, and the increment coefficient (used in Table 2) are shown.

	Initial species	Final species	Increment coefficient (Final/Initial)	Modern revisions and subsequent publications of new species
Afroxyidris	0	1		Belshaw and Bolton (1994)
Agraulomyrmex	0	2		Prins (1983)
Ankylomyrma	0	1		Bolton (1973b, 1981b)
Anochetus	24	18	0.75	Brown (1978)
Aphomomyrmex	2	1	0.50	Snelling (1979b)
Apomyrma	0	1		Brown, Gotwald and Levieux (1971)
Atopomyrmex	2	3	1.50	Bolton (1981b); Snelling (1992)
Axinidris	3	13	4.33	Shattuck (1991)
Baracidris	0	2		Bolton (1981b)
Bondroitia	3	2	0.67	Bolton (1987)
Calyptomyrmex	13	16	1.23	Bolton (1981a)
Camponotus (*fulvopilosus*-group)	2	4	2.00	Robertson (1990); Robertson and Zachariades (1997)
Cardiocondyla	11	9	0.82	Bolton (1982)
Cataulacus	38	39	1.03	Bolton (1974a, 1982); Snelling (1979a)
Concoctio	0	1		Brown (1974a,b)
Cyphoidris	1	4	4.00	Bolton (1981b)
Decamorium	2	2	1.00	Bolton (1976)
Dicroaspis	2	2	1.00	Bolton (1981a)
Diplomorium	1	1	1.00	Bolton (1987)
Dolioponera	0	1		Brown (1974c,d)
Leptogenys	32	56	1.75	Bolton (1975a)
Leptothorax	11	11	1.00	Bolton (1982)
Melissotarsus	6	3	0.50	Bolton (1982)
Meranoplus	9	8	0.89	Bolton (1981a)
Messor	14	14	1.00	Bolton (1982); Collingwood (1993)
Microdaceton	3	2	0.67	Bolton (1983)
Monomorium	90	149	1.66	Bolton (1987)
Ocymyrmex	12	37	3.08	Bolton (1981b); Bolton and Marsh (1989)
Odontomachus	1	2	2.00	Brown (1976)
Paedalgus	3	9	3.00	Bolton and Belshaw (1993)
Petalomyrmex	0	1		Snelling (1979b)
Platythyrea	15	14	0.93	Brown (1975)
Plectroctena	13	17	1.31	Bolton (1974b); Bolton, Gotwald and Leroux (1979)
Polyrhachis	43	47	1.09	Bolton (1973a)
Pristomyrmex	6	5	0.83	Bolton (1981b)
Probolomyrmex	3	3	1.00	Taylor (1965); Brown (1975)
Pyramica	24	63	2.63	Bolton (1983), Bolton (1999)
Psalidomyrmex	8	6	0.75	Bolton (1975b)
Rhoptromyrmex	3	5	1.67	Bolton (1976, 1986)
Simopone	7	9	1.29	Brown (1975); Kutter (1976, 1977)
Sphinctomyrmex	1	2	2.00	Brown (1975)
Strumigenys	17	42	2.47	Bolton (1983), Bolton (1999)
Terataner	5	6	1.20	Bolton (1981b)
Tetramorium	131	209	1.60	Bolton (1976, 1980, 1985)
Total	561	843	1.50	

Table 2. Afrotropical ant genera that have not received a modern taxonomic revision. The number of estimated species after revision was calculated by multiplying the number of valid species currently known by the Increment coefficient (1.5) in Table 1. The minimum years to revise a genus is calculated on the basis that B. Bolton processed species (i.e. the number of species before a revision) at a rate of 42/year.

Genus	Number of valid species	Estimated species after revision	Years (minimum) to revise genus
Acropyga	2	3	0.05
Aenictogiton	7	11	0.17
Aenictus	34	51	0.81
Amblyopone	3	5	0.07
Anoplolepis	19	29	0.45
Asphinctopone	3	5	0.07
Camponotus (excl. *fulvopilosus*-group)	156	234	3.71
Carebara	11	17	0.26
Cataglyphis	1	2	0.02
Centromyrmex	5	8	0.12
Cerapachys	24	36	0.57
Crematogaster	129	194	3.07
Cryptopone	1	2	0.02
Discothyrea	7	11	0.17
Dorylus	57	86	1.36
Ecphorella	1	2	0.02
Hypoponera	36	54	0.86
Lepisiota	45	68	1.07
Leptanilla	3	5	0.07
Myrmicaria	22	33	0.52
Mystrium	1	2	0.02
Oecophylla	1	2	0.02
Oligomyrmex	33	50	0.79
Pachycondyla	53	80	1.26
Paratrechina	13	20	0.31
Phasmomyrmex	4	6	0.10
Pheidole	66	99	1.57
Pheidologeton	7	11	0.17
Phrynoponera	5	8	0.12
Plagiolepis	18	27	0.43
Prionopelta	3	5	0.07
Proceratium	5	8	0.12
Pseudolasius	5	8	0.12
Santschiella	1	2	0.02
Solenopsis	10	15	0.24
Streblognathus	1	2	0.02
Tapinoma	13	20	0.31
Technomyrmex	25	38	0.60
Tetraponera	32	48	0.76
Total	862	1293	20.52

valid species currently known from the Afrotropical region.

Estimation of total species richness.—The percentage of undescribed species within recently revised genera is 30.9% for ants in Mkomazi Game Reserve and 32.3% for ants in Cape of Good Hope Nature Reserve (Table 3), remarkably similar values considering the distance between the two localities, the differences in their habitat complements and differing histories of ant collecting in the two regions. If these percentages are extrapolated to the unrevised genera, and the 50% increase from revis-

Table 3. Ant species diversity and composition in Mkomazi Game Reserve in Tanzania, Cape of Good Hope section of the Cape Peninsula National Park (CGH) in South Africa, and in the Afrotropical region as a whole.

	Mkomazi	CGH	Total	Afrotropical
All general:				
Total recorded species	232	72	303*	1705
Revised genera:				
No. widespread species	54	2	56	249
No. localized species	11	19	30	594
Total known species	65	21	86	843
% localized species	16.9	90.5	34.9	70.5
No. undescribed species	29	10	39	?
Total species	94	31	125	?
% undescribed species	30.9	32.3	31.2	?

* Only one species (*Technomyrmex albipes* (F. Smith)) shared between the two localities.

ing genera is taken into account, then the percentage of undescribed species for all genera is 44% for Mkomazi Game Reserve and 45% for Cape of Good Hope. Further collecting and analysis of ants at these localities is still taking place so the percentages above could change. There are considerable differences between the two localities in the proportion of known species in revised genera that have localised distributions covering only one or two countries (Table 3). Whereas only 16.9% of known species in Mkomazi Game Reserve have localised distributions, 90.5% of species in Cape of Good Hope Nature Reserve are localised. Many of the Mkomazi species are widely distributed in African savannahs, often ranging from the northern regions of South Africa through to Ethiopia or with a Sahel distribution from West Africa to Ethiopia and down into East Africa (Robertson 1999). The forest dwelling species also often have distributions extending into central Africa and other countries in East Africa. Conversely, many of the species in the Cape of Good Hope section of the Cape Peninsula National Park are limited to the Cape fynbos, or have distributions that extend only as far as Namaqualand or KwaZulu-Natal. In the Afrotropical region as a whole, 70.5% of species are localised (Table 3).

Based on the combined data from both Mkomazi Game Reserve and Cape of Good Hope, simple extrapolation of the proportion of undescribed species (using the formula $U = uK/k$) produces an estimated total of 3105 species for the Afrotropical region, whereas exclusion of the widespread species in the calculation of new species (using the formula $U = uL/l$) increases the total by 32% to produce an estimated total of 4093 species (Table 4). The estimated diversity using the latter formula on only the Mkomazi data is 6104 species, twice as high as the estimate based on only Cape of Good Hope, caused by the large difference between them in the ratio of widespread to localised species.

Based on the combined data from both localities, approximately 45–58% of ant species in the Afrotropical region are undescribed or are currently ranked as subspecies when they should be ranked as species (Table 4).

Accumulation of described species as a function of collecting date.—Analysis of the accumulation of described, valid species as a function of collecting date (Fig. 1) shows that undescribed species are being discovered at an undiminishing rate, with the species accumulation curve showing no signs of plateauing. The curve shows that

Table 4. Estimates of total ant species diversity in the Afrotropical region, based on the proportion of undescribed species in Mkomazi Game Reserve in Tanzania and in Cape of Good Hope section of the Cape Peninsula National Park (CGH) in South Africa (Table 3). The first estimate uses the ratio of total known species at a regional and local level and the second the ratio of localized known species (defined here as species that have been recorded from only one or two countries) at a regional and local level (see Methods for explanation of formulae).

	Estimated using data from:		
	Mkomazi	CGH	Both sites
1. Revised genera, based on total known species			
No. undescribed species (=uK/k)	376	401	382
Total species	1219	1244	1225
Ratio Total/Known	1.4462	1.4762	1.4535
2. Revised genera, based on localized species			
No. undescribed species (=uL/l)	1566	313	772
Total species	2409	1156	1615
Ratio Total/Known	2.8577	1.3709	1.9160
Estimated total species in all genera[1]			
Based on (1) above	3089	3153	3105
Based on (2) above	6104	2928	4093
% new species or species currently at infraspecific rank[2]			
Based on (1) above	44.8	45.9	45.1
Based on (2) above	72.1	41.8	58.3

[1] = (Total estimated revised species) × (Total/Known). Total estimated revised species = 843 + 1293 = 2136 (See Tables 1 & 2).

[2] = ((Estimated − Known)/Estimated) × 100. The number of known species = 1705.

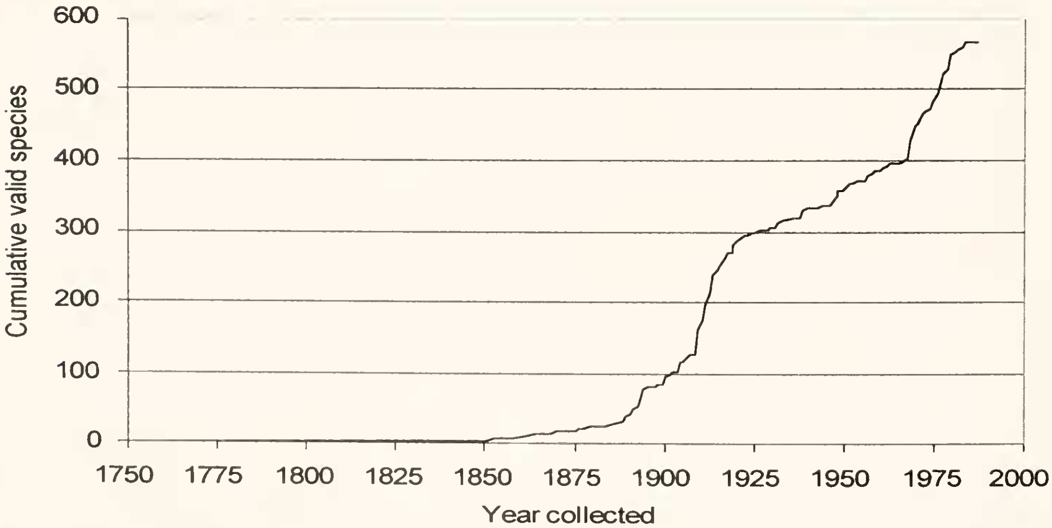

Fig. 1. Accumulation of new Afrotropical species in selected genera in relation to collection date of the type (publication date used where collection date absent). Information from Bolton (1974a, 1980, 1981a, 1981b, 1982, 1983, 1987). Only revisions from 1980 onwards included except for *Cataulacus* (Bolton 1974a) which was updated in the 1982 publication.

Table 5. Number of ant species revised and described by B. Bolton over a 16 year period (includes an extra year to account for the preparation time for the 1973 publications). Initial species refers to the number of valid species before the revision began. Average number initial species processed per year = 672/16 = 42.

Year published	Initial species	No. new species	No. species after revision
1973	43	10	48
1974	29	7	33
1975	67	29	88
1976	63	14	72
1977	52	37	86
1978	0	0	0
1979	23	17	38
1980	102	63	176
1981	55	23	74
1982	87	16	81
1983	44	65	107
1984	0	1	1
1985	0	0	0
1986	0	0	0
1987	107	46	167
Total	672	328	971

there was a burst of collecting from 1910 to 1925, overlapping with the period when George Arnold was mainly active. Following this burst, species accumulation increased at a slower rate until the 1970's when a new generation of ant collectors started using collecting techniques such as pitfall trapping, tree fogging and Winkler bag leaf litter extractions that produced species that had previously gone undetected. These techniques are still yielding many new species and additional techniques such as soil sifting should start tapping into the subterranean species that are still poorly known.

Time taken to revise genera.—Over a 16-year period, Barry Bolton revised genera that initially contained a total of 672 species, amounting to processing 42 initial species per year (Table 5). The total of 971 species after revision amounts to describing and characterising a species every four working days. Over such a long period and taking into account other concerns and responsibilities, this is a formidable rate of species processing that is unlikely to be equalled or bettered by anyone working at an equivalent level of thoroughness.

Based on Bolton's level of productivity, it would take about 21 years for one person to revise the remaining unrevised genera (Table 2). The genera *Camponotus, Crematogaster, Dorylus, Lepisiota, Pachycondyla* and *Pheidole* would each take more than a year to revise.

DISCUSSION

Afrotropical ant species richness.—The method presented here, that of excluding widespread species in calculating the proportion of new species, has not been presented before and is an attempt (following on Hodkinson and Hodkinson 1993) to address the problem of differences in the average geographical distribution of known and undescribed species. The estimate of 4093 Afrotropical ant species produced by using this method is 32% greater than the 3105 species estimated using the conventional ratio of undescribed to all known species. These estimates could be improved if more sites are included.

In total, therefore, 45–58% of species are undescribed or currently incorrectly placed at subspecific rank. This range of values compares favourably with the 52% unknown species, calculated from Hölldobler and Wilson's (1990) estimate of 20000 species world-wide and the actual number (at the end of 1993) of 9538 species determined by Bolton (1995a). Shattuck (1999) states that the Australian ant species diversity might well be double that currently known, which also matches the estimates presented here for the Afrotropical region. At a local level, Watt *et al.* (1997) estimated that 40% of the ants they captured in Mbalmayo Forest Reserve in southern Cameroon were undescribed which compares favourably with the 44–45% undescribed species for all genera recorded at the two localities in the present study.

On the basis that 18% of the world's described ant species are found in the Afrotropical region (calculated from Bolton 1995a), the species diversity estimates presented here can be extrapolated to a world level to give an estimated world diversity of between 17250 and 22739 species. However, as the Nearctic and Palaearctic ant faunas are much better known than those from other regions, the 18% Afrotropical ant species is likely to be an underestimate.

Progress with sampling of ants in Africa.— Awareness about the threats to biodiversity have increased funding for inventory-based conservation research and as ants are a favoured indicator taxon (Andersen 1997), there has been a consequent tremendous recent growth in ant collections. Intensive sampling projects in the Afrotropical region include: Mbalmayo Forest Reserve in southern Cameroon (Watt *et al.* 1997); coastal and interior forest in Gabon (Fisher, in prep.); Mkomazi Game Reserve in Tanzania (Robertson 1999); Cape of Good Hope, Robben Island, Brenton-On-Sea, Fairfield Farm near Napier, Kogelberg Biosphere Reserve, and other sites in the Cape fynbos, South Africa (Robertson and co-workers, in prep.); Cape indigenous evergreen forests (Fisher, in prep.); Mondi Estate in Kwazulu-Natal (Fisher, in prep.); and widespread pitfall trapping by E. Marais in Namibia. However, there are still enormous gaps in our coverage. Countries such as Angola, Mozambique, Malawi, Zambia, Central African Republic, Ethiopia and Sudan have yet to be sampled using modern inventory techniques. Even the best sampled countries such as South Africa and Zimbabwe remain patchily sampled and there is not one country in the Afrotropical region where ants have been sampled adequately in all major vegetation regions.

Future strategies for collecting.—The best approach to adequately sampling the ants of a large area such as the Afrotropical region is through intensive inventory-based sampling of particular localities by general collecting and a combination of replicated pitfall trapping, Winkler bag leaf litter extractions, beating or sweeping of vegetation, chemical knockdown of arboreal fauna and soil sampling. The use of replicable sampling methods makes it possible to statistically compare sites using techniques described in Colwell & Coddington (1994) and Chazdon *et al.* (1998) and in this way to make scientifically based assessments of alpha, beta and gamma diversity. Fisher (1996, 1998, 1999) has pioneered this approach in Madagascar although only for leaf litter and ground fauna. Recent studies, still unpublished (e.g. Fisher and Robertson in prep. for a site near Ambositra in Madagascar), have used a wider range of replicated sampling techniques. Superficial general collecting of many localities is of more limited value than the inventory approach although it is useful for providing distributional data. As ants are dominant and ecologically important organisms in terrestrial ecosystems, growth of collections will also continue due to the submission of specimens by ecologists and agricultural researchers for identification by ant systematists.

Inventory-based assessments of areas for conservation using ants will ensure continued funding of scientifically-based ant collecting in the Afrotropical region, provided there remains backup by ant systematists. The areas to be sampled will be largely dictated by the conservation funding bodies and by the political stability of the areas that need assessment. Notwithstanding the political issues, the neglected countries such as those listed above, need attention. With this increased ant collecting, the need for more taxonomic work on ants will become all the more apparent.

Current progress with Afrotropical ant taxonomy.—Based on relative proportion of species, we are about 39% of the way through revision of the Afrotropical ant genera to modern standards and to revise the remaining genera would take one person 21 years to complete at 'Bolton speed'.

On a world level, there are about 41 people currently working on the taxonomy of ants. Although this seems a large number, the productivity of most of these taxonomists is much less than that of B. Bolton and their work is often limited to regional faunas. In addition, a number of our key established 'global view' systematists have either recently retired or are about to retire. We could end up with a situation similar to that in termite taxonomy (Eggleton 1999) although we are likely to remain stronger in terms of number of systematists.

The low taxonomic productivity of most ant systematists can be attributed largely to their occupation with other endeavours: ecological and biological research on their study organisms, administration, contract identification work, computer programming, and teaching duties. Revising ant genera at the rate that B. Bolton has achieved is therefore rarely attained and for most systematists one would need to settle for a speed of revision at best half or even quarter of Bolton's rate. However, there is room for improvement and I feel that ant systematists need to prioritise alpha taxonomy and not let it take a back seat which seems to be increasingly the case.

Unlike the situation in North America, Europe, South America and Asia, there is only one resident ant systematist in Africa and hence progress with documenting Afrotropical ants will depend largely on the involvement of outside 'global-view' systematists working on taxa that are represented in the Afrotropical region.

Strategies for advancing Afrotropical ant taxonomy.—The two goals of a strategy to improve ant taxonomy are firstly, to ensure that the number of ant systematists does not dwindle but remains stable or grows and secondly, to improve the effectiveness and productivity of current ant systematists. Regarding the first aspect, it is vital that the museums holding important ant collections are committed to employing ant systematists. It is remarkable that the most important ant collection in the world at the Harvard Museum of Comparative Zoology has no full-time ant systematist committed to alpha taxonomy and has a curator that can work only part-time on this vital collection. The Natural History Museum in London, with the second largest ant collection in the world, should continue its support of a position in ant systematics once the present incumbent retires. The South African Museum holds the largest ant collection in Africa and should also remain committed to supporting ant systematics, especially as it is important to maintain an ant identification service for applied entomologists in Africa.

Training is an important aspect of safeguarding the future body of ant systematists because filling of positions in systematics is usually controlled more by the quality of the candidate than by the group he/she works on. Hence, the contribution to training by ant systematists at universities is essential to the future growth of ant systematics.

Regarding the second component in the strategy, there are five ways in which the effectiveness and productivity of current ant systematists could be improved: (1) In order to cope with the conflict between projects geared to collection growth as opposed to taxonomic projects, we need to make the latter a priority and plan time to spend on them. For instance, university lecturers often find it easiest to plan time for taxonomic work over the long vacations. (2) Dedicated funding of ant taxonomic revisions along the same lines as the Australian Biological Resources funding for catalogues, in which money is allocated in proportion to the size of the taxon, would be ideal for improving goal-setting and productivity. In reality, this type of funding is rare because a taxonomic revision does not answer applied problems directly. (3) A more realistic approach to obtaining funding for ant taxonomy would be to link it to more easily obtained funding for applied field-based projects. Funding from these projects can be used for employing and training parataxonomists for time-consuming sorting, mounting and curation of ants. Funding bodies should commit themselves to permitting a direct taxonomic component in the project so that there are funds to employ people to measure specimens and funds to visit overseas ant collections to examine types. Funding should also be built into these projects for storage and curation of the specimens. (4) There is a great need for training of, and exchange of ideas between, established ant systematists, especially the large number residing outside North America and Europe. Better communication via e-mail would help, but the funding of one or more training and planning meetings would be ideal. (5) As there is still so much work to be done in revising all Afrotropical ant genera (at least 21 man-years), it is important to prioritise groups for revision. In the Afrotropical region, the unrevised groups encountered most frequently when identifying ants are *Pheidole*, *Crematogaster* and *Camponotus*. These groups also happen to be among the most diverse of the unrevised genera (Table 2) and are also among the most difficult taxonomically, either because of worker polymorphism (*Pheidole* and *Camponotus*) or because of a paucity of external morphological species-discriminating characters (*Crematogaster*). Not surprisingly therefore, these groups have been avoided and to get them done quickly it would be best to develop a funded strategy.

Ants are an economically and ecologically important group in terrestrial ecosystems in the Afrotropical region and improving their taxonomy would in turn improve the networking of ecological, agricultural and behavioural ant research. The present study provides the information for planning a funded strategy to document the Afrotropical ant fauna. The challenge is to create a synergy between the different role players (systematists, ecologists, funding bodies) so that individual efforts are not swamped by the immensity of the job at hand.

ACKNOWLEDGMENTS

I thank Brian Fisher for his comments on the manuscript and the following organisations and individuals for helping with field work and processing of samples: Royal Geographical Society, Tanzanian Department of Wildlife, Simon van Noort, Tony Russell-Smith, Daniel Mafunde, Omari Mohamed, Tandi Russell, Dawn Larsen, Cape Peninsula National Park (and prior to its formation, the management of the Cape of Good Hope Nature Reserve) and Miemsie Troskie.

LITERATURE CITED

Andersen, A. 1997. Ants as indicators of ecosystem restoration following mining: a functional group approach. Pp. 319–325 in P. Hale and D. Lamb (eds) *Conservation Outside Nature Reserves*. Brisbane: University of Queensland.

Arnold, G. 1915–1924. A monograph of the Formicidae of South Africa. *Annals of the South African Museum* 14: 1–766.

Arnold, G. 1926. A monograph of the Formicidae of South Africa. Appendix. *Annals of the South African Museum* 23: 191–295.

Belshaw, R. and B. Bolton 1994. A new myrmicine ant genus from cocoa leaf litter in Ghana (Hymenoptera: Formicidae). *Journal of Natural History* 28: 631–634.

Bolton, B. 1973a. The ant genus *Polyrhachis* F. Smith in the Ethiopian region (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 28: 283–369.

Bolton, B. 1973b. A remarkable new arboreal ant genus (Hym. Formicidae) from West Africa. *Entomologist's Monthly Magazine* 108: 234–237.

Bolton, B. 1974a. A revision of the palaeotropical arboreal ant genus *Cataulacus* F. Smith (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 30: 1–105.

Bolton, B. 1974b. A revision of the ponerine ant genus *Plectroctena* F. Smith (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 30: 309–338.

Bolton, B. 1975a. A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian region with a review of the Malagasy

species. *Bulletin of the British Museum (Natural History). Entomology* 31: 235–305.
Bolton, B. 1975b. A revision of the African ponerine ant genus *Psalidomyrmex* André (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 32: 1–16.
Bolton, B. 1976. The ant tribe Tetramoriini (Hymenoptera: Formicidae). Constituent genera, review of smaller genera and revision of *Triglyphothrix* Forel. *Bulletin of the British Museum (Natural History). Entomology* 34: 281–379.
Bolton, B. 1980. The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History). Entomology* 40: 193–384.
Bolton, B. 1981a. A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History). Entomology* 42: 43–81.
Bolton, B. 1981b. A revision of six minor genera of Myrmicinae (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History). Entomology* 43: 245–307.
Bolton, B. 1982. Afrotropical species of the myrmicine ant genera *Cardiocondyla, Leptothorax, Melissotarsus, Messor* and *Cataulacus* (Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 45: 307–370.
Bolton, B. 1983. The Afrotropical dacetine ants (Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 46: 267–416.
Bolton, B. 1985. The ant genus *Triglyphothrix* Forel a synonym of *Tetramorium* Mayr (Hymenoptera: Formicidae). *Journal of Natural History* 19: 243–248.
Bolton, B. 1986. A taxonomic and biological review of the tetramoriine ant genus *Rhoptromyrmex* (Hymenoptera: Formicidae). *Systematic Entomology* 11: 1–17.
Bolton, B. 1987. A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History). Entomology* 54: 263–452.
Bolton, B. 1994. *Identification Guide to the Ant Genera of the World*. Cambridge, Massachusetts: Harvard University Press, 222 pp.
Bolton, B. 1995a. A taxonomic and zoogeographical census of the extant ant taxa (Hymenoptera: Formicidae). *Journal of Natural History* 29: 1037–1056.
Bolton, B. 1995b. *A New General Catalogue of the Ants of the World*. Cambridge, Massachusetts: Harvard University Press, 504 pp.
Bolton, B. 1999. Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). *Journal of Natural History* 33: 1639–1689.
Bolton, B. and R. Belshaw 1993. Taxonomy and biology of the supposedly lestobiotic ant genus *Paedalgus* (Hym.: Formicidae). *Systematic Entomology* 18: 181–189.
Bolton, B., W. H. Gotwald Jr. and J. M. Leroux 1979 ("1976"). A new West African ant of the genus *Plectroctena* with ecological notes (Hymenoptera: Formicidae). *Annales de l'Université Abidjan. Série E (Écologie)* 9: 371–381.
Bolton, B. and A. C. Marsh 1989. The Afrotropical thermophilic ant genus *Ocymyrmex* (Hymenoptera: Formicidae). *Journal of Natural History* 23: 1267–1308.
Brown, W. L. Jr. 1974a. *Concoctio* genus nov. *Pilot Register of Zoology* Card No. 29.
Brown, W. L. Jr. 1974b. *Concoctio concenta*. *Pilot Register of Zoology* Card No. 30.
Brown, W. L. Jr. 1974c. *Dolioponera* genus nov. *Pilot Register of Zoology* Card No. 31.
Brown, W. L. Jr. 1974d. *Dolioponera fustigera* species nov. *Pilot Register of Zoology* Card No. 32.
Brown, W. L. Jr. 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini. *Search. Agriculture (Ithaca, N. Y.)* 5(1): 1–115.
Brown, W. L. Jr. 1976. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomologica* 19: 67–171.
Brown, W. L. Jr. 1978. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section B. Genus *Anochetus* and bibliography. *Studia Entomologica* 20: 549–638.
Brown, W. L. Jr., W. H. Gotwald Jr. and J. Lévieux 1971 ("1970"). A new genus of ponerine ants from West Africa (Hymenoptera: Formicidae) with ecological notes. *Psyche (Cambridge)* 77: 259–275.
Chazdon, R. L., R. K. Colwell, J. S. Denslow and M. R. Guariguata 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. Pp. 285–309 in F. Dallmeier and J. A. Comiskey (eds) *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*. Paris, France: Parthenon.
Collingwood, C. A. 1993. Description of the host ant of *Cossyphodinus bremeri* Ferrer sp. nov. (Hymenoptera, Formicidae). Pp. 229–231 in J. Ferrer and C. A. Collingwood, New species of *Cossyphodinus* from Africa (Coleoptera, Tenebrionidae) and description of the host ant *Messor ferreri* sp. nov.

(Hymenoptera, Formicidae). *Entomofauna* 14: 221–232.

Colwell, R. K. and J. A. Coddington 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences* 345: 101–118.

Eggleton, P. 1999. Termite species description rates and the state of termite taxonomy. *Insectes Sociaux* 46: 1–5.

Fisher, B. L. 1996. Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana: Zoology* 85: 93–108.

Fisher, B. L. 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the Western Masoala Peninsula, Madagascar. *Fieldiana: Zoology* 90: 39–67.

Fisher, B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. *Ecological Applications* 9: 714–731.

Gauld, I. and B. Bolton (Eds) 1988. *The Hymenoptera.* Oxford: Oxford University Press, xii + 322 pp.

Hammond, P. M. 1995. Described and estimated species numbers: an objective assessment of current knowledge. Pp. 29–71 in D. Allsopp, R. R. Colwell and D. L. Hawksworth (eds) *Microbial Diversity and Ecosystem Function.* Wallingford, UK: CAB International.

Hodkinson, I. D. 1992. Global insect diversity revisited. *Journal of Tropical Ecology* 8: 505–508.

Hodkinson, I. D. and D. Casson 1991. A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society* 43: 101–109.

Hodkinson, I. D. and E. Hodkinson 1993. Pondering the imponderable: a probability-based approach to estimating insect diversity from repeat faunal samples. *Ecological Entomology* 18: 91–92.

Hölldobler, B. and E. O. Wilson 1990. *The Ants.* Cambridge, Massachusetts: Harvard University Press, xii + 732 pp.

Kutter, H. 1976. Beitrag zur kenntnis der gattung *Simopone* Forel. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 49: 273–276.

Kutter, H. 1977. Zweiter beitrag zur kenntnis der gattung *Simopone* Forel. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 50: 173–176.

Prins, A. J. 1983. A new ant genus from southern Africa (Hymenoptera, Formicidae). *Annals of the South African Museum* 94: 1–11.

Robertson, H. G. 1990. Unravelling the *Camponotus fulvopilosus* species complex (Hymenoptera: Formicidae). Pp. 327–328 in G. K. Veeresh, B. Mallik and C. A. Viraktamath (eds) *Social Insects and the Environment. Proceedings of the 11th International Congress of IUSSI, 1990.* New Delhi: Oxford & IBH Publishing Co.

Robertson, H. G. 1999. Ants (Hymenoptera: Formicidae) of Mkomazi. Pp. 321–336 in M. Coe, N. McWilliam, G. Stone and M. J. Packer (eds) *Mkomazi: the Ecology, Biodiversity and Conservation of a Tanzanian Savanna.* London: Royal Geographical Society (with the Institute of British Geographers).

Robertson, H. G. and C. Zachariades 1997. Revision of the *Camponotus fulvopilosus* (De Geer) species-group (Hymenoptera: Formicidae). *African Entomology* 5: 1–18.

Shattuck, S. O. 1991. Revision of the dolichoderine ant genus *Axinidris* (Hymenoptera: Formicidae). *Systematic Entomology* 16: 105–120.

Shattuck, S. O. 1999. *Australian Ants: their Biology and Identification.* Collingwood, Victoria: CSIRO Press, 226 pp.

Snelling, R. R. 1979a. Three new species of the Palaeotropical arboreal ant genus *Cataulacus* (Hymenoptera: Formicidae). *Contributions in Science (Los Angeles)* 315: 1–8.

Snelling, R. R. 1979b. *Aphomomyrmex* and a related new genus of arboreal African ants (Hymenoptera: Formicidae). *Contributions in Science (Los Angeles)* 316: 1–8.

Snelling, R. R. 1992. Two unusual new myrmicine ants from Cameroon (Hymenoptera: Formicidae). *Psyche (Cambridge)* 99: 95–101.

Taylor, R. W. 1965. A monographic revision of the rare tropicopolitan ant genus *Probolomyrmex* Mayr (Hymenoptera: Formicidae). *Transactions of the Royal Entomological Society of London* 117: 345–365.

Ward, P. S., B. Bolton, S. O. Shattuck and W. L. Brown, Jr. 1996. *A Bibliography of Ant Systematics.* Berkeley: University of California Press, 417pp.

Watt, A. D., N. E. Stork, P. Eggleton, D. Srivastava, B. Bolton, T. B. Larsen, M. J. D. Brendell and D. E. Bignell 1997. Impact of forest loss and regeneration on insect abundance and diversity. Pp. 274–286 in A. D. Watt, N. E. Stork and M. D. Hunter (eds) *Forests and Insects.* London: Chapman and Hall.